Biometric variables predict stone tool functional performance more effectively than tool-form attributes: a case study in handaxe loading capabilities

Alastair J. M. Key [1]*, Stephen J. Lycett [2]

[1] School of Anthropology and Conservation, University of Kent, Canterbury, CT2 7NR, UK

[2] Department of Anthropology, University at Buffalo, SUNY, Amherst, NY 14261, USA

* Corresponding author: a.j.m.key@kent.ac.uk, +44(0)1227 827056

Abstract

Both the form of a stone tool, and the anatomy of the individual using it, have potential to influence its cutting performance. To date, however, the selective pressures acting on stone-tool form and hominin biometric/biomechanical attributes have been investigated in isolation and their relative influence on performance have never been compared directly. Here, we examine the influence of both tool-form attributes and biometric variation on the functional performance of Acheulean handaxes. Specifically, we investigate the impact of 13 tool attributes and eight biometric traits on the working forces applied through the edge of 457 replica tools. The relative contribution of tool-form and biometric attributes to handaxe loading levels were examined statistically. Results identify that both tool-form attributes and biometric traits are significantly related to loading, however, tool-user biometric variation has a substantially greater impact relative to tool-form attributes. This difference was demonstrated by up to a factor of ten. These results bear directly on the co-evolutionary relationships of stone tools and hominin anatomy, and the comparative strength of selective pressure acting on each. They also underline why handaxe forms may have been free to vary in form across time and space without necessarily incurring critical impacts on their functional capabilities.

Keywords: Acheulean; ergonomics; cutting force; biface, Lower Palaeolithic, selective pressure

1. Introduction

Archaeologists and anthropologists often seek to reconstruct how efficiently lithic artefacts could have been used by Plio-Pleistocene hominins (Schick and Toth, 1993; Shea, 2007; Marzke, 2013; Key and Lycett, 2017a). Two analytical routes are typically used to investigate this. The first examines the morphology of stone tools recovered from the archaeological record and interprets how efficiently or effectively they could have been used during cutting tasks. The second relies on reconstructing the biomechanical capabilities and comparative tool-use abilities of fossil hominins. Beyond the invaluable data derived from artefact and fossil morphologies, both routes rely heavily on experimental programs undertaken using modern human subjects.

Experimental research over the past 40 years has, for example, demonstrated that the performance characteristics (sensu Schiffer and Skibo, 1997) of flake stone tools are influenced by their size, edge morphology and sharpness (Walker, 1978; Jobson, 1986; Prasciunas, 2007; Key and Lycett, 2014, 2015; Key et al., 2018). Others have demonstrated that edge curvature and regularity influence the performance of scraping tools (Collins, 2008; Clarkson et al., 2015), while size, edge angle, and potentially symmetry, can influence the functional capabilities of Acheulean bifaces (Jones, 1981; Machin et al., 2007; Key et al. 2016; Key and Lycett, 2017b). In other words, it has been demonstrated that some tool-form attributes can have a strong and statistically significant impact on a stone tool's performance characteristics.

Similarly, experimental data have demonstrated that an individual's biomechanical capabilities and biometric traits can impact the efficiency and effectiveness of stone tool use. Marzke and Shackley (1986) were among the first to demonstrate how anatomical features of the hand, including a strong, relatively long thumb were linked to the performance of hand-held stone tools. Key and Lycett (2018) have more recently demonstrated how the strength and dimensions of tool user's hands are correlated with the cutting performance of flake tools and handaxes, with different biometric traits contributing to tool efficiency in variable ways dependent on the type of tool used. Rolian et al. (2011) also demonstrated a negative relationship between the length of a tool user's digits and the muscular force required to stabilize joints during 'simulated stone tool use'. Work by Hamrick et al. (1998) and Williams-Hatala et al (2018) further emphasizes the high muscular recruitment and loading required by the thumb and index finger during effective flake and handaxe use. Other work has examined fossil evidence, with the aim of identifying the influence that stone tool production and use likely had on hominin manual anatomy (Marzke, 1997, 2013; Kivell, 2015).

Given such work, it is now well established that both the form of a stone tool and the biometric traits of the individual using it can influence its functional performance. Both types of variable affect performance via their influence on ‘cutting stress’, which is created in a worked material by the tool’s cutting edge (Atkins 2009). Cutting stress, calculated as force per unit area ($\sigma = N/m^2$), dictates whether an edge can create a fracture (i.e. cut) in a worked material. The greater the stress, the more likely it is that material bonds will be broken (Atkins 2009). The morphology of a stone tool’s cutting edges (e.g. edge radii, angle, curvature) influence cutting stress by altering the amount (area) and morphology of the edge in contact with the material being cut and, moreover, how forces are distributed through this edge (Ackerly, 1978; Atkins, 2009; Key, 2016). Overall tool-size and shape attributes, meanwhile, affect the ergonomic nature of the tool, how precisely it may be applied during cutting, and how much force is required to stabilize the tool in the hand, as well as the length of utilizable cutting edge (Jones, 1981; Hall, 1997; Seo and Armstrong, 2008; Toth and Schick, 2009; Rossi et al., 2014; Wynn and Gowlett, 2018; Key et al., in press). The biomechanical capabilities of tool users may similarly impact force application, tool stabilisation and movement, and cutting precision. This can be realized through the amount of muscular force created by the tool user and transferred through joint surfaces, which in turn, changes the forces conveyed through the tool and onto the worked material. Alternatively, there can be variation in the opposability of manual aspects and the ease with which tools can be securely gripped when resisting use-related forces, or when rotating and manipulating tools (Marzke and Shackley, 1986; Rolian et al., 2011; Seo and Armstrong, 2008; Key and Lycett, 2018).

An understanding of how the working-force capabilities of stone tools is influenced by independent variables are, then, essential to understanding how they create cutting stress and their eventual efficiency during use. In particular, the performance attribute of ‘loading’ (i.e., the creation of force normal and parallel to the worked material) and its role in the creation of cutting stress is a parameter that is key to understanding the relative efficacy of prehistoric cutting tools (Atkins, 2009), including butchery processes, woodworking, digging for tubers, scraping hides, among others. Indeed, functional interpretations of individual morphological traits in an absence of their known influence on force creation, diminishes our understanding of that cutting tool’s potential performance or capabilities.

If, as is often argued (Jones, 1981; Isaac, 1981; Shea, 2007; Key and Lycett, 2017a), the functional performance of stone cutting tools was of concern to Plio-Pleistocene hominins and had potential to impact resource acquisition, survival and—ultimately—reproductive success, then variables facilitating greater cutting stress could have been positively selected for. Given the foregoing, this could have been achieved through selection on hominin biomechanical attributes and/or on tool forms. Indeed, it has been argued that functional selective pressures were likely influencing the form of lithic artefacts produced by Plio-Pleistocene hominins (e.g. Crompton and Gowlett, 1993; Diez-Martín et al., 2014; Borel et al., 2017; Key and Lycett, 2017a; Wynn and Gowlett, 2018). Moreover, effective and efficient stone tool use requirements are widely thought to have affected the evolutionary trajectory of hominin hand anatomy during this period (Marzke and Shackley, 1986; Marzke, 1997, 2013; Hamrick et al., 1998; Kivell, 2015; Rolian et al., 2011; Key and Lycett, 2018; Williams-Hatala et al., 2018). Previous investigations into the role of loading on stone tool performance have principally been focused on projectile velocities and consequences of impact (Hutchings, 2011; Milks et al., 2016), the pressures and forces distributed through tool-users' digits (Rolian et al., 2011; Williams-Hatala et al., 2018), and the use of force sensitive cells beneath portions of cut material (Key and Lycett, 2014, 2015). To date, however, the selective pressures acting on tool-form and biometric/biomechanical attributes have been investigated in isolation and their relative strength of influence have never been compared directly.

This study aims to investigate the relative influence of biometric variation and tool-form variation on the loading capabilities of Acheulean handaxes. An understanding of the comparative influence of both artefactual and biological variables on stone tool performance can help to identify the relative strength of forces acting on evolutionary changes in both hominins and tools. Furthermore, such data can aid our understanding of how free biological and cultural elements were to vary without there being critical implications for the functional performance of stone implements. In turn, such considerations are important when interpreting morphological variation in fossil hominin upper limb anatomy and the Palaeolithic archaeological record. If biometric traits are determined to be significantly more influential than tool-form attributes, for example, it could be hypothesized that any variation observed in handaxes is relatively arbitrary in terms of predicting their functional capabilities, with hominin anatomy being the more critical factor. Here, we examine the influence of variation in both tool-form attributes and biometric traits on the loading capabilities of 457 replica Acheulean handaxes. Specifically, we investigate how the working forces applied through the cutting edges of these replica bifaces are influenced by 13 tool-form attributes and eight biometric traits on a comparative basis.

2. Materials and methods

2.1 Participants and Biometric Traits

Participants were sourced from the student population at the University of Kent. A total of 46 participants were recruited, with a female-to-male ratio of 9:14. Each individual had eight biometric traits recorded on their dominant hand. Using digital calipers, 'Hand Length' was recorded in millimetres (mm) from the tip of the third digit to the first (most proximal) crease line at the wrist. The 'Digit Length' of the thumb, index and middle fingers were similarly recorded using digital calipers from the tip of each respective digit to the inferior crease line at its intersection with the hand. First-to-second digit ratios ('1D:2D') were calculated for all participants by dividing the first digit length by the second. 'Grip Strength' was recorded in a transverse hook grip, in kilograms (kg), using a hand dynamometer. 'Pad-to-Side Pinch Strength', where the participant's distal palmar aspect of the thumb opposed the lateral side of the 2nd digit, was recorded using a hydraulic pinch gauge (kg). 'Tip-to-tip Pinch Strength' was recorded using the same gauge (kg), with the participant's distal palmar aspects of digits one and two forcefully opposing. Descriptive statistics for all biometric traits are detailed in Table 1. Participants provided informed consent and were aware of the task conditions, items involved and general theme of the research before taking part. Participants were not aware of the specific hypotheses under investigation.

2.2 Replica Handaxe Assemblage and Tool Form Attributes

The replica handaxe assemblage was produced by AK (480) and SL (20) using flint sourced from Suffolk and Kent (UK). Hard and soft (antler) hammer percussion were used. In total, 500 handaxes were produced, with each of the 46 participants being randomly assigned 10 handaxes that were used in a randomized order, with an original intention to use a total sample of 460 handaxes for the experiment. However, due to participant #13 having to cease their participation in the experiment unexpectedly early, they only used seven handaxes, meaning that the final utilized assemblage consisted of 457 replica tools (Fig. 1).

Detailed below are the 13 morphological attributes recorded from each tool. In all instances, the superior surface is defined as the face displaying the largest number of flake scars above 5 mm^2 (Lycett et al., 2006).

- 'Mass' was recorded in grams using digital scales.
- 'Length' was recorded in mm using digital calipers and was defined as the maximum distance measured on a handaxe when viewed from the superior surface.
- 'Width' was defined as the maximum distance between the two lateral edges of a handaxe on the superior surface when directly perpendicular to its line of maximum symmetry (see below), and was recorded in mm using digital calipers.
- 'Thickness' was recorded in mm using digital spreading calipers and was defined as the maximum depth of a handaxe at any point perpendicular to both Length and Width.
- 'Shape' was examined using a size-adjusted (scale-free) dataset of 29 morphometric variables recorded from plan and side view photos of each handaxe (following: Lycett et al., 2006). Using these metrics, Principal Component Analysis was used to describe the major patterns in shape variation within the assemblage. Here, shape is defined by PC1.
- 'Position of Maximum Width' was calculated as the position at which Width was recorded longitudinally on each tool, expressed as a percentage of Length (from tip [0%] to base [100%]).
- 'Position of Maximum Thickness' was calculated as the position at which Thickness was recorded longitudinally on each tool, expressed as a percentage of Length (from tip [0%] to base [100%]).
- 'Width/Length' ('Elongation') was calculated by dividing the aforementioned Width measurement by Length.
- 'Thickness/Width' ('Refinement') was calculated by dividing the aforementioned Thickness measurement by Width.
- 'Percentage of Edge Flaked' is a scale-free measurement of how much of a tool's circumference (when in plan view) displayed a sharp, flaked edge. This was achieved by uploading an image of each tool's superior surface into the freeware Image J. Once the scale was set, the 'freehand' draw and 'measure' functions were used to record both the total circumference of the tool's edge and the length of flaked edge, from which the Percentage of Flaked Edge could be calculated.

- 'Edge Uniformity' is a measure of edge irregularity as it undulates from the tip of a handaxe to its base. A side-profile image of each handaxe was uploaded into 'Image J', from which, two measurements were taken. The first recorded the length of a straight line between the two distal ends of the cutting edge. The second measures the true length of the edge as it tracks up and down from the tool's tip to its base. Straight line length is then divided by the true length of the edge, to create a value between 0-1 describing Edge Uniformity.
- 'Edge Angle' is a record of the angle produced between the two intersecting surfaces of a biface as they join to form an edge. Edge angles from 20 locations on each tool (tip, base, and at 10% intervals of length on both lateral edges) were recorded using the 'caliper technique' (Dibble and Bernard, 1980), with the mean of these being used as the overall measure of Edge Angle. Angles were only recorded from flaked edges (i.e. not from those retaining cortex).
- 'Bilateral Symmetry' is a measure of handaxe symmetry between the two lateral sides of a tool (recorded across a tool's longitudinal midline). It was calculated here using the 'Index of Symmetry' outlined by Lycett et al. (2006), where the distal (tip) end of the line used to record Length is used as a locked landmark and a straight line with equal maximum distances from the left and right edges of the tool is drawn, with this being the line of symmetry. Perpendicular distances from this line to the left and right edges of each handaxe were then recorded at 10% intervals of the line's length. Counterpart left and right measurements were used to calculate the symmetry index using the following equation :

$$S = \sum_{i=1}^{n} \left(\sqrt{\frac{(x_i - y_i)^2}{(x_i + y_i)}} \right),$$

  where x_i equals the width left of the maximum symmetry line and y_i corresponds to the width right of the line. An index value of zero would describe complete symmetry, while higher values quantify relative levels of deviation from perfect symmetry. The sum of the nine individual measures of symmetry was averaged.

These metrics have previously been linked with the functional performance of handaxes during cutting tasks (Jones, 1981; Gowlett, 2006, 2013; Machin et al., 2007; Grosman et al., 2011; Key and Lycett, 2017a). Descriptive statistics for all metrics are presented in Table 2.

2.3 Experimental Task

Previous experimental research investigating the loading capabilities of hand-held stone tools recorded normal force (kgf) during linear cutting actions (Key and Lycett, 2014, 2015). Experimental research inevitably involves some trade-off between realism and the extent of imposed experimental controls, which are necessary for scientific rigor, but which invariably impinge on realism (Eren et al. 2016). Determining a reasonable strategy to negotiate these opposing strengths and weaknesses, must primarily be based on the specifics of the questions being addressed in any given case. Given the aims of the present research, we deliberately used an experimental task that was absent of 'slicing' (c.f. Atkins et al., 2004) to more precisely focus on tool-user and tool-morphology interactions and how they specifically impact on loading force levels, rather than using a task that involved cutting motions or involved the dynamics of interaction between the tool and material being cut.

To this end, we used a hinged wooden platform similar to that used in previous stone-tool loading research (Key and Lycett, 2014; Stemp et al., 2015). This was comprised of an upper wooden board suspended horizontally, above a lower, larger wooden board (Fig. 2). The upper board was attached to the lower via a hinge at one end, while the other end had a hard rubber stud suspended beneath it. The rubber stud rested directly on top of a Tekscan ELF Force System^{TM} sensor. Opposing the rubber stud, on the superior side of the wooden board, was a metal bolt nut (10 mm in diameter). The metal nut was the point of contact between the handaxe and the loading platform (Fig. 2). Hence, when tool users applied force through a handaxe's edge, they did so onto the metal bolt, with this force being transferred directly through the rubber stud and onto the force sensor. Force was recorded here in kilogram-force (1 kgf = ~9.8 N) at a rate of 20Hz. The greatest force recorded during any loading event was used as the representative datum for that loading event. Loads were applied for 3-5 second periods. Participants were asked to apply as great a load as possible through the handaxe and onto the metal bolt.

One of the benefits of this protocol is the ability to directly control where loads are applied along the cutting edge of a handaxe, something not possible in standard cutting tasks. To this end, participants exerted force through five distinct points along the edge of each tool. These were determined by percentage intervals at 0-5%, 20%, 40%, 60% and 80% of a handaxe's length. The mean of the five recorded forces were used here as a record of the force (kgf) applied by participants through the edge of each tool. The order that percentile points along the edge were used was randomly assigned for each participant using www.randomizer.org. This prevented any potential confounding influence from fatigue.

Due to the potential influence that the body's position can have on loading levels during tool use (McGorry et al., 2004) the force platform was placed on a desk in front of participants while they were seated. To ensure this position was consistent, all participants adjusted the height of the chair so that their navel was level with the top of the desk, their non-dominant hand was placed on the desk next to the lower board and both feet were kept on the floor at all times. Participants were directed not to rise from a seated position at any point. Should any of these requirements be broken, participants were required to cease exerting force and the tool was re-applied. While this is not a body position likely to have regularly been used by handaxe wielding Plio-Pleistocene hominins, it does appropriately focus data collection on the loading levels achievable by the upper limb of hominins, while minimizing body mass differences and cutting-motion variation among participants.

The available ergonomic literature provides evidence of links between the grips used to secure a hand-held tool and subsequent achievable working loads and gripping forces (Hall, 1997; Seo and Armstrong, 2008; Rossi et al., 2014). In turn, additional points of task standardization were imposed. Following previously published analyses of grip variation during the use of handaxes (Marzke and Shackley, 1986; Key et al., in press), all participants were limited to using grips where the thumb and fingers secured the handaxe on opposing sides of the tool and contact point between the palm and handaxe may go no further than 50% of the handaxe's length away from the tool's base (Fig 3). Participants were permitted to balance their index finger on the upper edge of the handaxe if they preferred (Fig. 3b, 3c). Several types and variants of grips conform to these restrictions, which together account for upwards of 85% of manual positions used during handaxe use (Key et al., in press). Particularly small handaxes were able to be held with a pad-to-side precision grip (Marzke and Shackley, 1986; Key et al., in press). All handaxes, no matter how large, were required to be held with a single (dominant) hand. Grips were free to vary when loading different edge point locations, so long as the above conditions were met. Since participants were only applying force during the experiment rather than using the handaxes in an actual cutting motion, they were not required to use gloves. However, all participants were informed that should they experience any discomfort, they must cease tool loading immediately.

2.4 Statistical Analysis

Backwards stepwise regression (BSR) was used to identify which of the eight biometric and 13 tool-form attributes contributed proportionately more towards the prediction of loading forces in handaxes, relative to other variables. First, a BSR was run with all 21 variables, before being repeated independently for just the eight biometric and 13 tool-form attributes. BSR begins by placing all predictors (biometric and tool-form traits) into a regression analysis and calculates the contribution of each to the model's prediction of force. If a variable is not making a significant contribution to the model then it is removed and the model is re-estimated with the remaining predictors. This continues on a stepwise basis until only variables that make a significant contribution to the model's prediction remain. Effectively, an 'order of contribution' is produced, with R^2 values indicating the relative strength of relationships between independent variables and handaxe forces. Stepping criteria used entry and removal values of 0.001 and 0.005, respectively. These low criteria values allowed the production of an order of contribution despite a relatively large number of variables potentially displaying a significant relationship with loading levels. In effect, forced BSR models were run.

The three most important biometric traits and tool-form attributes to the determination of handaxe loading capabilities, as determined by the stepwise regressions, were investigated using standard linear regression. These regressions were run to establish the predictive (explanative) power of each variable, and whether, independently, they significantly influenced the force applied by tool users. Essentially, the production of these independent linear regressions allowed assessment of the predictive power of individual traits irrespective of when removed from the BSR, as their early (forced) removal from the model may obfuscate their independent predictive power. Individual R^2 values were then compared between tests to establish whether biometric or tool-form variables are more important to the determination of handaxe working force. Significance was determined in accordance with the Bonferroni Correction for multiple tests, such that $\alpha = .008$.

3. Results

Across all 457 handaxes, a mean maximum force of 3.84 kgf was recorded. There was, however, substantial variation in the forces recorded, with standard deviation equalling 4.10

kgf and the coefficient of variation, expressed as a percentage, equalling 107 %. Loading ranged from 0.33 kgf (~ 3.2 N) to 24.24 kgf (~ 237.7 N). In short, there was substantial variation in the forces applied through a handaxe's cutting edge, but across all participants these averaged around 4 kgf (~ 39.2 N).

Table 3 details the results of the BSR containing the eight biometric traits and 13 tool-form attributes. The five strongest predictive variables of handaxe loading are biometric traits, with the final stepwise model (model 20) containing both Grip Strength and Pad-to-Side Pinch Strength (despite the low entry and removal criteria). Not only does this indicate the biometric traits of tool users to be the most important criteria in the determination of handaxe working loads, but the relative strength, and in particular precision pinching strength, of tool users are the most important traits. First-to-second digit ratio, and the respective length of the first and second digits are, respectively, the third, fourth and fifth strongest predictors of force. Edge Angle makes the sixth greatest contribution towards the prediction of handaxe loading levels, and is the strongest predictive variable of all tool-form attributes. The first nine variables removed from the model are all tool-form attributes, indicating that a broad range of these variables have little to no influence on handaxe loading levels.

The entry of all eight biometric variables into a BSR produced 7 model steps, with two predictive variables remaining in the final model, despite the very low entry and removal criteria (Supplementary Table 1). R^2 values indicate that when modelled collectively, a substantial proportion of the loading variation observed can be explained as a result of the biometric variation observed in tool users (up to 51%). The two traits remaining in the final model were Grip Strength and Pad-to-Side Pinch Strength, which were inseparable in terms of their contribution to the prediction in loading levels, with 49% of the normal force variation explained by these two attributes. First-to-second digit ratio was the third strongest predictive variable, followed by the lengths of digits one through three. Tip-to-tip Pinch Strength and Hand Length were the first two attributes removed from the model. It is important to note that early removal from this model does not mean that traits do not have a significant impact on handaxe loading levels, just that they make a weaker contribution to the prediction of handaxe loading levels relative to traits in later models.

The 13 tool-form attributes, when entered into a BSR, resulted in 13 model steps (Supplementary Table 2). Edge angle was the only predictive variable to remain in the final model. R^2 values were substantially reduced relative to the biometric variables, with tool-form attributes explaining <6% of the loading variation in all models. Position of Maximum Width, Shape, and Elongation were the second, third and fourth strongest predictive variables, although it should again be stressed that they made a relatively low contribution. In sum, although an order of contribution has been produced, with Edge Angle making the greatest contribution towards the prediction of handaxe force capabilities, it appears the tool-form attributes examined here have a limited impact on handaxe loading.

Differences between the predictive power of biometric and tool-form traits are also highlighted by the individual linear regressions run with the three strongest predictors of handaxe loading for each type of trait (Table 4). The only tool-form attribute to significantly predict handaxe loading levels was again demonstrated to be Edge Angle, while all three biometric traits returned statistically significant values. There was also a marked difference in the strength of R^2 values in the two types of variable (Table 4). Indeed, between 20–48% of loading variation can be explained by the three biometric traits, while <3% of applied force can be explained by tool-form attributes.

4. Discussion

Variation in tool-user biometric traits and tool-form attributes have both been demonstrated to influence the functional performance of stone tools (Walker, 1978; Jobson, 1986; Prasciunas, 2007; Collins, 2008; Key and Lycett, 2018; Clarkson et al., 2015). 'Loading' is a crucial variable in the performance of a cutting tool (Atkins, 2009; Key 2016), being directly related to the generation of 'cutting stress' (force per unit area). Presented here are data investigating the comparative influence that biometric variables and tool-form variables have on the loading capabilities of Acheulean handaxes. Although handaxe effectiveness has long been a point of interest in experimental archaeology studies (e.g., Leakey, 1950; Jones, 1981; Machin et al., 2007; Shea, 2007; Toth and Schick 2009; Galán and Domínguez-Rodrigo, 2014), loading has not previously been examined in these tools. Our data reveal that tool-user biometric variation can have a substantially greater impact on loading relative to tool-form attributes. This difference is demonstrated here by up to a factor of up to ten.

Collectively, these results highlight that not all variables relevant to the efficient and effective use of stone tools are equally influential. In turn, we contend that when considering how effectively Palaeolithic hominins were able to use handaxes, an individual's ability to forcefully secure, grip and manipulate these tools was by far the most important factor, relative to the morphology of the tool being used. Effective handaxe use was, therefore, influenced to a greater extent by the biometric condition and biomechanical capabilities of the hominin using the tool, relative to the form of the tool itself.

The disparity observed here is particularly surprising given the coefficient of variation levels present in each category of variable. Ordinarily, in terms of prediction, it would be expected that the independent variable(s) exhibiting the greatest levels of variation would show higher levels of correlation with the dependent variable. As revealed in Tables 1 and 2, however, the variation observed in the tool-form attributes is, in most instances, greater than those seen in the biometric traits. Despite the greater variation in many of the tool-form attributes, it is the biometric traits, with their relatively lower CV levels, that have greater impact on loading. These data, therefore, further underline the importance of a tool user's biometric condition when considering stone-tool functional performance.

Our data support previous research emphasising areas of functionally related 'free play' in handaxe morphology, where variation in form has a potentially limited impact on performance (Isaac, 1972; Crompton and Gowlett, 1993: 177; Lycett et al., 2016). Indeed, previous research has indicated that shape, size, and symmetry (Machin et al., 2007; Key and Lycett, 2017b) have only limited impact on a handaxe's ability to be used as a cutting tool; at least until morphological 'thresholds' are reached (Key and Lycett, 2017b). As experimentally confirmed elsewhere, however, some specific tool form attributes do have significant influences on stone tool performance (e.g., Clarkson et al., 2015; Key et al., 2018). Further, we acknowledge that the present analyses are absent of the dynamic motions required during cutting actions, with some variables potentially being of greater relevance during such motions (e.g., Simão, 2002; Gowlett, 2006). This includes the length and uniformity of a handaxe's cutting edge, where the sweeping motion used in some cutting actions could have a greater impact than observed here where the focus is on loading. Moreover, a few handaxes at the upper extremes of the size variation, while serviceable in a downward plane, may become unwieldy with one hand when used in more complex motions. Nonetheless, a stone tool's loading potential is a relevant and important factor in determining its functional performance, and investigation of the variables influencing this metric is vital to understanding the capabilities of stone tools in prehistory. Our data suggest, therefore, that the selective pressures on handaxe form relating to loading potential would be relatively low, allowing for substantial variation in the range of tool morphologies produced by Acheulean hominins. The considerable variation observed in archaeological handaxe forms across different sites (e.g., Wynn and Tierson 1990; Chauhan 2010; Gowlett, 2013; Norton et al., 2006; Petraglia and Shipton, 2009; Lycett and von Cramon-

Taubadel, 2015), and even within individual sites (e.g., Crompton and Gowlett, 1993; Gowlett, 2006, 2013; Archer and Braun, 2010; Wang et al., 2014; Moncel et al., 2016), also supports the notion that hominins likely had a relatively large degree of freedom when producing functionally viable bifaces (at least for a majority of traits).

Our finding that edge angle significantly influences handaxe loading levels is consistent with previous research detailing its impact on biface cutting performance. As demonstrated by Key et al. (2016), the relationship between handaxe edge angle variation and cutting performance is complex and depends on both the ease of cutting stress creation between the tool and worked materials, and the tool user's ability to exert high working loads through the tool. Our data speak to the latter side of that equation, and indicate that more obtuse edges on handaxes facilitate the exertion of greater loading levels by tool users' hands onto the tool. This additional force is then transferred through the tool and onto the worked material. Indeed, the more obtuse the edge, the greater the tool's surface area in contact with the hand, and the lower the stress exerted by the tool on the skin (therefore reducing the risk of injury and pain). Previous suggestions (e.g., Gowlett 2006; Grosman et al., 2011; Key et al., 2016) that Acheulean hominins intentionally produced the more obtuse base ('butt') edges observed on handaxes in response to ergonomic considerations are, therefore, strengthened by the present data.

Our data also reaffirm the significant and strong impact that biometric variation in a tool-user's hands can have on the functional performance of stone tools. Previous works by Rolian et al. (2011) and Key and Lycett (2018) have demonstrated how variation in the size, strength, and digit ratios of an individual's hands have potential to influence how effectively Lower Palaeolithic stone tools can be used, and the subsequent impact on cutting performance. Here, we demonstrate that loading potential, a previously under-investigated performance characteristic, is also significantly and strongly influenced by biometric variation in the hand. Most notably, individuals with increased precision-grip strength capabilities can apply significantly greater force through handaxes during their use. For hominin populations where stone tool use was important to their survival, it is therefore reasonable to hypothesize that those individuals able to more capably apply stone tools could have had a selective advantage, and the phenotype underpinning this capability would have been passed to successive generations.

It is important to acknowledge that the present results were generated from a sample of individuals displaying modern human (Homo sapiens) hand anatomy and corresponding levels of biometric variation. Given that the precision-gripping capabilities of H. sapiens are hypothesized to have been selectively favoured over millions of years (Tocheri et al., 2008; Marzke, 2013; Kivell, 2015), it is arguably the case that the participant sample used here displays lower levels of variation than that observed in early tool using populations; potentially indicating the observed relationships to have been stronger during the Lower Palaeolithic. Differences in hand anatomy between modern humans and Lower Palaeolithic hominin species do, however, raise questions about how accurately results can be applied to prehistoric populations. Fossil hand remains from the earliest hypothesized tool-using hominin species (> 2 Mya) often indicate a transitional anatomy, with some human-like precision manipulative capabilities (Tocheri et al., 2008; Kivell, 2015). While hand remains from between ~1.8–0.3 Mya are rare, those available indicate additional modern human-like features (Dominguez-Rodrigo et al., 2015; Lorenzo et al., 2015), such as the styloid process on the third metacarpal (Ward et al., 2014). Hence, while it is not yet precisely clear how different modern human and Acheulean hominin hand anatomy is, we would argue based on these known similarities, that the relationships observed here can also be attributed to Acheulean species. Irrespective of the hand anatomy of handaxe using hominins, however, there would have been variation on the population level, against which selective pressures could have acted.

Finally, the loading ranges recorded here are substantial, with up to ~24 kgf being exerted through a handaxe. Although such high values were rare, with only seven individuals recording mean forces of 10 kgf or above for at least one of their utilized tools, it is arguably the case that the modern, relatively sedentary, lives of the participants restricted the number of individuals able to exert higher loads. While these forces are unlikely to be applied during typical 'slice push' cutting motions (Atkins et al., 2004; Atkins, 2009), as observed when slicing through animal flesh, for example, it is nonetheless clear that substantial forces can be applied through a handaxe's working edge. Other cutting activities that more heavily depend on load application in single plane, such as forcing apart joint sockets or digging tubers from the ground, may profit from the exertion of particularly high loads. This would indicate that ruling out hypothesized functions for handaxes based solely on their requirement for high working loads is not necessarily justified.

5. Conclusion

Here, we demonstrate that biometric attributes, most notably an individual's precision-grip strength, more readily predict handaxe loading levels relative to tool-form variables. Indeed, up to ~50% of the force applied through the cutting edge of a handaxe can be attributed to the biometric condition of the individual using that tool. Multiple regression of 13 tool-form attributes could only account for ~5% of a handaxe's loading potential. Predictive models of Acheulean handaxe functionality should, therefore, take greater account of the anatomy and manipulative capabilities of the individual using the tool, relative to the form of the tool being used. Moreover, the selective pressures acting on both hominin anatomy and stone-tool morphology were likely to have been disparate during the Palaeolithic. Overall, these results help explain the derived, precision-and-manipulation focused hand anatomy observed in H. sapiens. They also, however, underline why archaeological handaxe forms may have been free to vary in form across time and space without necessarily incurring critical impacts on their functional capabilities.

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